EDGE EFFECTS ON CORTICOLOUS COLLEMBOLA IN RICHMOND PARK (UK)

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ABSTRACT

Edge effects are thought to affect many woodland life forms, but there are few studies on edge effects in corticolous springtails (Collembola). This project used vacuum collections of springtails from tree bark (1–2 m elevation) to test for edge effects along 64 m transects in four plantations within Richmond Park, London over four seasons in 2015. The biggest factor affecting collembolan populations was found to be season (with numbers peaking in winter), along with the depth of bark crevices (with highest numbers in the deepest crevices). The two commonest springtails, *Orchesella cincta* (L.) and *Entomobrya albocincta* (Templeton), showed significant woodland-edge avoidance. The dataset included far more specimens of *Entomobrya corticalis* (Nicolet) (128) than all previous reliable UK records combined (2), almost entirely off old oaks *Quercus robur* L. Unexpectedly almost no specimens of the locally dominant (putatively invasive) corticolous species *Entomobrya intermedia* Brook were collected, instead finding many *Entomobrya nivalis* (L.). These findings are the first report of an edge-effect in corticolous springtails, and also suggest that the woods of Richmond Park are harbouring a relic springtail community, isolated by the extensive acid grassland around them.

INTRODUCTION

Edge effects, as defined by Laurance & Yensen (1991), are properties of ecotones across the junction between two dissimilar habitat types (Ewers & Didham, 2006). Both biotic and abiotic variables can display a response to edges (Stevens & Husband, 1998; Gehlhausen, Schwartz & Auspurger, 2000; Laurance, 2000; Kotze & Samways, 2001). Many previous studies in this area have concentrated on abiotic variables across forest and field boundaries, in particular changes in light intensity, temperature and relative humidity along transects (Kapos, 1989; Chen, Franklin & Spies, 1992; Murcia, 1995; Turton & Freiburger, 1997; Newmark, 2001). Light, temperature and wind speed usually decrease in a predictable way towards the centre of wooded areas whilst humidity should increase (Murcia 1995; Chen *et al.,* 1999). Hence microclimate is predicted to vary with distances from the edge of a plantation. The type of boundary may exert an effect, with abrupt edges resulting in sharp gradients whilst more typically diffuse edges give shallower gradients (Weathers, Cadenasso & Pickett, 2001).

Edge effects have been studied for many life forms, from lichens (Esseen & Renhorn, 1998) and litter invertebrates (Didham, 1997) to top-level carnivores (Balme, Slotow & Hunter, 2010), and extend up to 150 m from a forest edge boundary for some primates (Lenz, Jack & Spironello, 2014). Edge effects on species distribution are rarely as smooth as for meteorological data. Dangerfield *et al.* (2003) studied the terrestrial insect communities across a boundary between saltbush and riparian zones, and found habitat-specific species 'leaked' over the boundary giving a mixed community either side of the actual boundary. Helle & Muona (1985) studying clear-fell edges in Finland found that Hymenoptera, Arachnida and Gastropoda were commonest around the boundary, declining in both directions away from the edge. Foggo *et al.* (2001) found distinct canopy communities on either side of a boundary between two tropical forest types, but no clear edge-associated community.

Although Collembola are generally animals of moist habitats, with poor control of water loss (Hopkin, 1997), there is a well-defined group of species that are habitually found in corticolous/canopy habitats. In the UK this group is dominated by species in the genus *Entomobrya*, along with *Orchesella cincta* (L.) (see Plate 1 for examples). *Entomobrya albocincta* (Templeton) is so consistently reported from corticolous sites (eg Elbourn, 1970; Hingley, 1971; Lambert, 1973; Bowden, 1976; Prinzing, 2001, 2005; Shaw *et al.,* 2007; Shaw, 2015) that their occasional discovery in soil cores under dense woodland (eg Shaw & Usher, 1997) probably reflects animals that have fallen out of the canopy. *Entomobrya corticalis* (Nicolet) is invariably collected from bark (Fjellberg, 2007), but appears to be scarce in the UK. *Entomobya nivalis* (L.) is also a typical canopy springtail (eg Prinzing, 2005; Shaw *et al.,* 2007) but is also found commonly in the soil surface (Waldorf, 1980; Leinass, 1983; Shaw & Usher, 1997). *Orchesella cincta* is also well known to be arboreal (Van der Woude & Verhoef, 1986; Shaw *et al.,* 2007). Other corticolous Collembola genera include *Anurophorus, Vertagopus* and *Willowsia* (Hopkin, 2007), but a variety of other species have been collected sporadically from canopy faunas, including 'edaphic' species such as *Protaphorura armata* (Tullberg) (Shaw *et al.,* 2007). Collembola are major contributors to vertical migration on woodland trees (Farrow & Greenslade, 1992; Majzlan & Fedor, 2003), although it is still unclear to what extent there is a net upward traffic implicitly being offset by animals falling back to the soil (Shaw, 2015).

It seems *a-priori* plausible that the UK bark springtail community will vary with tree species, as has been shown for other canopy arthropods (e.g. Ozanne, 1999 showed differences between the canopy fauna of conifers and broadleaved trees in the UK.) Lambert (1973) observed differences between the bark fauna of oak and pine (with *Entomobrya nivalis* being confined to pine bark). Ozanne (1996) and Shaw *et al.* (2007) compared canopy faunas of two conifers, *Picea* and *Pinus*, both finding differences but in different directions: Ozanne (1996) reported higher densities of Collembola in the canopy of *Pinus,* while Shaw *et al.* (2007) found higher densities in Sitka spruce *Picea sitchensis* (Bong.) Carrière although there were no consistent differences in community composition.

Corticolous arthropods are sensitive to microclimate. Work by Prinzing (e.g. 2001, 2005) showed that the distributions of the collembolans *Orchesella cincta, Entomobrya nivalis* and *Entomobrya albocincta* (along with other bark fauna) living on the bark of isolated trees followed microclimatic patterns, and that they used bark crevices as refuge from unsuitable conditions (a form of compensatory behaviour). Bowden, Haines & Mercer (1976) observed that most vertical migration by springtails occurred from 1700 h to 1000 h, presumably to reduce the risk of desiccation.

There are few papers on the responses of canopy Collembola to edge effects, despite their known sensitivity to microclimatic fluctuations. Shaw *et al.* (2007) found no edge effects in Collembola of coniferous canopies, despite clear edge effects in simultaneous meteorological data. Here we present results from a survey designed to seek edge effects in bark-dwelling Collembola from plantation woodland within a partly-medieval deer park, along with micro-climatic, tree-species and seasonal influences.

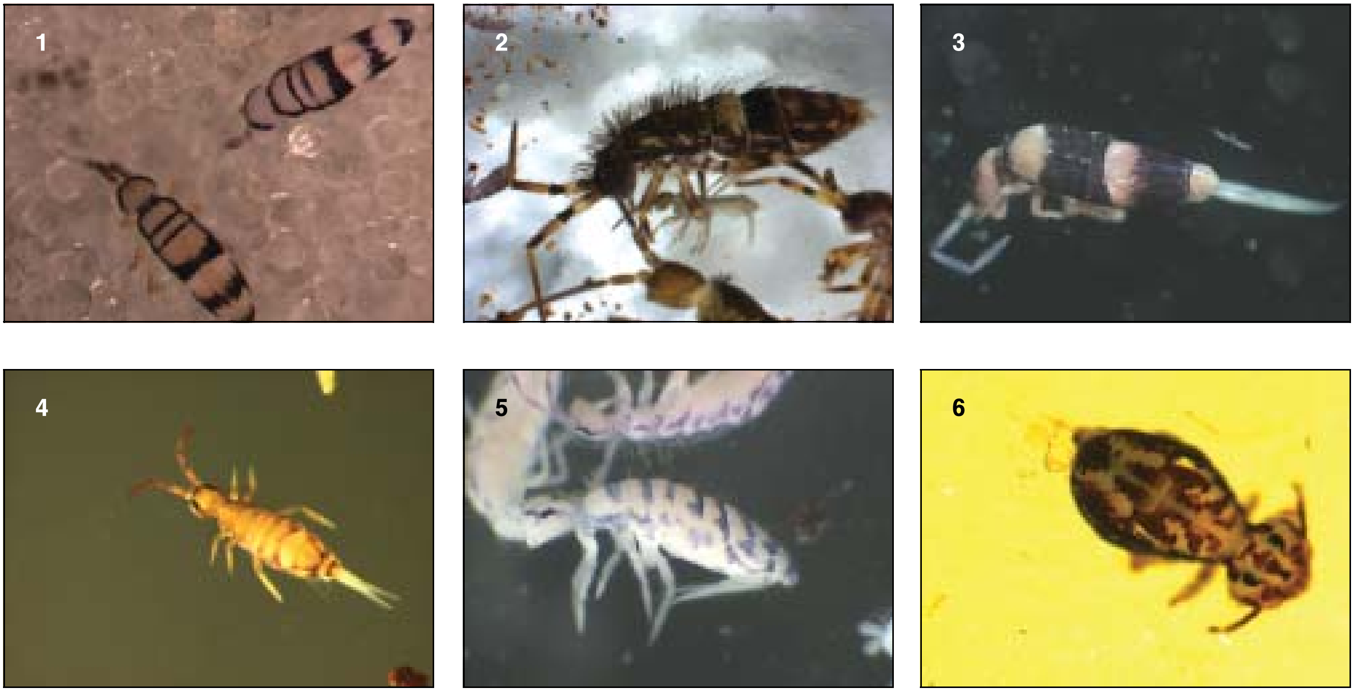

PLATE 00. Examples of corticolous Collembola in the UK. Fig. 1. *Entomobrya corticalis* (Entomobryidae). Fig. 2. *Orchesella cincta* (Entomobryidae). Fig. 3. *Entomobrya albocincta* (Entomobryidae). Fig. 4. *Entomobrya nivalis* (Entomobryidae). Fig. 5. *Entomobrya multifasciata* (Entomobryidae). Fig. 6. *Dicyrtomina saundersii* (Sminthuridae).

Table 1. Site descriptions of the four plantations studied. Area and perimeter calculated using a planimeter (Freemaptools, 2015) over satellite images of Richmond Park [source: Google Maps (2016)].

Site	Description	Area (ha)	Perimeter (m)	Ordnance Survey Grid reference
Site 1 Isabella (conservation area)	Fenced; no public access. Thick undergrowth [up to 1.5 m height in places], established *Quercus, Betula, Acer* and *Betula.*	5.5	1050	TQ1987372101
Site 2 Sawpit wood	Unfenced; on a hillock with a wide path separating the north and south sections. Mature *Quercus, Betula, Castanea, Aesculus*, frequently used by humans and two species of deer.	11.7	1600	TQ1997273648
Site 3 Sidmouth Wood	Fenced; some undergrowth. *Quercus, Acer, Betula, Aesculus*	19.3	1690	TQ1926673261
Site 4 Spanker's Wood	Unfenced; on a hillock. Mature *Quercus, Castanea* and *Pinus.* Frequently used by humans and two species of deer.	15.0	1590	TQ2080472722

Fig. 1. Sampling for bark-inhabiting Collembola using a hand-held Dyson vacuum cleaner.

MATERIALS AND METHODS

Site description

The site for this study, Richmond Park, London is a man-made deer park enclosed in 1637 by Charles I (Brown, 1985). It is a Site of Special Scientific Interest, National Nature Reserve and Special Area of Conservation (Natural England, 1992). The dominant habitat is acid grassland, with scattered woods dominated by mature/veteran oak trees, along with at least eight other tree species. Previous studies have shown it to support a high diversity of canopy invertebrates (Barnard, Brooks & Stork, 1986, Stork *et al.,* 2001). Four plantations were sampled (defined in Table 1). Collections were taken four times in 2015 (20 May, 1 September, 27 October, 11 December). On each occasion two replicate transects were taken from random starting locations in each of the four woods, making a total of 128 records.

Data collection

Tape was used to measure out 64 m transects on a logarithmic scale [1, 4, 16 and 64 m] from the edge of each plantation, with invertebrate samples taken from the closest tree to each collection point. Invertebrate samples were taken using vacuum sampling of the bark (Fig. 1), utilising a Dyson handheld vacuum at 1–2 m height using three sets of ten second bursts [equal to approx. $0.05m^2$ based on test runs using flour as a marker]. The samples were immediately transferred into labelled tubes, and preserved in 70% Industrial Methylated Spirits prior to manual sorting. The vacuum interior was brushed out between samples to minimise contamination. All Collembola were identified to species using Hopkin (2007). An anemometer [Casella M116008] and mercury thermometer were used for field meteorology. In each case three consecutive measurements were taken and the mean recorded. Additionally meteorological data (recorded every 30 minutes) for Richmond Park was kindly supplied by the Royal Parks staff. Crevice depth was measured as the depth of three replicate crevices randomly located on three trees per species using manual callipers with a probe attachment, resulting in one mean value (based on nine measurements) per tree species.

Statistical analyses

All analyses used in R 3.0.2. Individual species responses were mainly highly non-Gaussian so were tested using Kruskal-Wallis anova for differences between sites and dates, and their responses to edge effects + bark depth tested using Spearman's correlation coefficient. Where data were acceptably Gaussian (e.g. the log-transform of total Collembola density) they were analysed by GLM with wood and season as factors, bark depth and distance from edge as covariates. The best model was defined as the one with the lowest value of Akaike's Information Criterion (AIC), derived using the AIC function in R. This is an index based on estimating a maximum likelihood function for each model and penalising it for the number of parameters fitted (Akaike, 1981), and has gained popularity as an objective way to decide which is the best model in real (often complex) ecological studies (Johnson & Omland, 2004; Symonds & Moussalli, 2011). In this case these models also had the highest F values, though this is not always so.

RESULTS

Unsurprisingly, the meteorological data showed seasonal differences in temperature, light levels and humidity (with December being the coldest darkest and most

Table 2. Summary meteorological data for each sampling event at Richmond Park, London in 2015.

Date	Temperature sampled °C	Wind speed Sampled m/s	Temperature Park °C averaged 1 week	Humidity Park % averaged 1 week	UV dose Park J m^{-2} averaged 1 week
20 May 2015	16.2 ± 3.5	2.3 ± 4.4	11.3 ± 3.9	73.8 ± 16.6	0.19 ± 0.30
01 Sept 2015	16.4 ± 1.9	0.2 ± 0.9	15.74 ± 2.4	86.5 ± 11.0	0.09 ± 0.18
27 October	18.25 ± 1.2	1.2 ± 2.6	10.9 ± 3.1	87.9 ± 8.3%	0.01 ± 0.04
11 Dec 2015	9.5 + 0.6	3.9 ± 3.4	13.9 ± 1.9	94.6 ± 5.4	0.002 ± 0.002

humid month, May the least), but otherwise these data showed few noteworthy patterns. The only edge effect was wind speed, which declined smoothly and significantly away from the plantation edge (Fig 2; $r_s = -0.22$, df = 126, $p < 0.05$). Summary meteorological data for each sampling event are shown in Table 2.

Out of 6629 invertebrates recovered, 5128 were Collembola (77.4%). The 21 species of Collembola are listed in Table 3 along with summary statistics, showing that two species (*O. cincta* and *E. albocincta*) accounted for 60.7% of the total Collembola. Smaller numbers of rarer Collembola appeared, most notably a total of 128 *E. corticalis*, (previously specimens had been collected only from just two sites in the UK, both tree bark in the south east). The largest variation was seasonal: densities and species richness were both highest in December and lowest in May (Figs 3 and 4). Tree species was also a significant factor for some species: *E. corticalis* was almost confined to oak bark (113/128 animals, against 61 oaks/128 trees; $\chi^2_1 = 84.7$, $p < 0.001$), while *Entomobrya multifasciata* (Tullberg) was almost confined to pine and oak (850/856 on these two tree species comprising 69/128 trees; $\chi^2_1 = 709.4$ $p < 0.001$).

The two most common species, *O. cincta* and *E. albocincta*, were found to increase in density away from the plantation edge (Figs 5 and 6; both $p < 0.05$), as did total Collembola (but only at $p < 0.1$). When the edge-effect analyses were repeated for each season, edge avoidance was shown to be especially pronounced for *O. cincta* in November and December ($r_s = 0.36$ and 0.40 respectively; Table 4). Edge avoidance was also consistently found (though non-significant) in *E. albocincta*, but not in any other Collembola (Table 4).

Considering all Collembola combined, Kruskal-Wallis anova found only the effect of season to be significant (chi-squared with 3df = 72.3 and 58.7 for abundance and richness respectively), but using a GLM on log-transformed data, the best model for abundance was Season * Wood with bark depth as a covariate (Table 5), while Collembola species richness was best modelled by season with bark depth as a covariate (Table 5). Adding meteorological variables did not improve model fits.

Discussion

By far the commonest Collembola collected from these tree barks were *E. albocincta*, *E. nivalis*, *E. multifasciata* and *O. cincta*, all species that are widely encountered up trees in the UK (Elbourn, 1970; Lambert, 1973; Shaw *et al.;* 2007; Shaw, 2013; 2015). The next commonest species (with 128 specimens) was *E. corticalis,* well-documented as a bark-dwelling species in eastern, central and western mainland Europe (Pflug & Wolters, 2001; Fjellberg, 2007; Raschmanová,

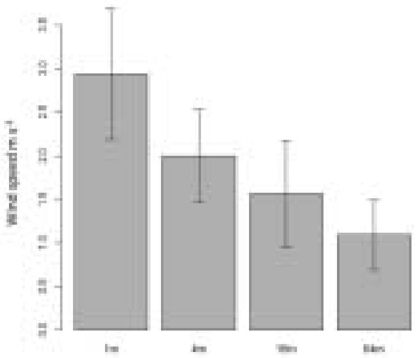

Fig. 2. The change in windspeed with distance from woodland edge, Richmond Park, 2015.

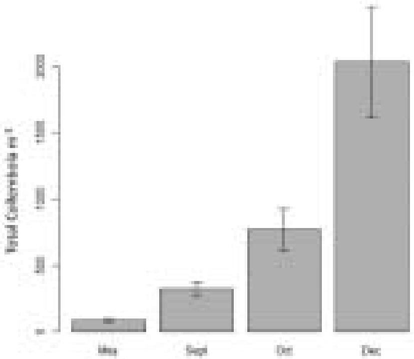

Fig. 3. Total Collembola m^{-2} against month, Richmond Park 2015.

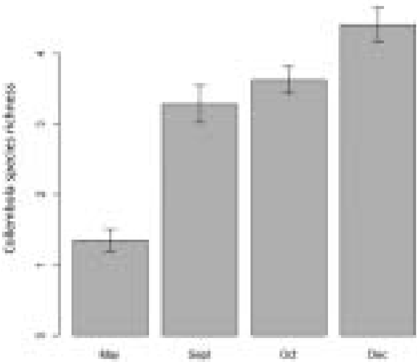

Fig. 4. Collembola species richness against month, Richmond Park 2015.

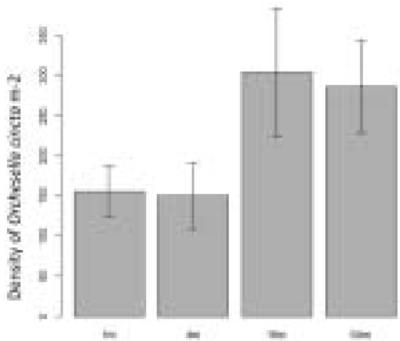

Fig. 5. Edge effect in *Orchesella cincta*, Richmond Park 2015.

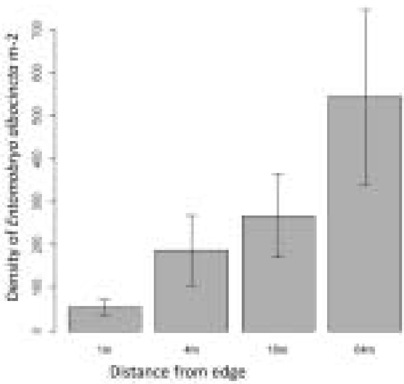

Fig. 6. Edge effect in *Entomobrya albocincta*, Richmond Park 2015.

Table 3. Summary data on all Collembola collected. Statistical tests were not performed for species with <10 captures.

Species	Density Mean ± SE	#captures (max 128)	Season? Chi sq 3df	Wood? Chi sq 3df	Edge effect (r_s, p)	Comment
Total Collembola	801.3 ± 129.6	121	**72.3*****	6.0NS	0.17 p = 0.07	Densest on oak and sweet chestnut, and in sites 2 and 4
Collembola sp richness	3.2 ± 0.2		**58.9*****	0.8NS	0.11NS	No clear patterns with respect to tree species or sites.
Allacma fusca (L.)	0.2 ± 0.2	1				
Anurophorus laricis Nicolet	14.2 ± 4.2	23	2.9 NS	7.3NS	0.1NS	Mainly found on sweet chestnut, never on pine
Cyphoderus albinus Nicolet	0.3 ± 0.3	1				
Dicyrtomina ornata (Nicolet)	0.7 ± 0.4	4				
Dicyrtomina saundersii (Lubbock)	3.2 ± 1.4	8				
Dicyrtoma fusca (Lubbock)	0.5 ± 0.3	2				
Entomobrya albocincta (Templeton)	223.9 ± 28.2	114	**30.8****	14.9**	0.20*	Highest density on oak and sweet chestnut
Entomobrya corticalis (Nicolet)	20 ± 7.5	21	NS	20.8***	0.07NS	Only in sites 1 and 3, mainly on oak.
Entomobrya nivalis (L.)	121.3 ± 17.4	87	**68.4****	4.7NS	0.01NS	
Entomobrya intermedia Brook	0.5 ± 0.3	2				
Entomobrya multifasciata Tullberg	136.1 ± 66.2	23	**10.1***	**18.3*****	-0.1NS	Only found on oak and pine in site 4
Entomobrya nicoleti (Lubbock)	2.7 ± 1.0	10	**11.8****	5.6NS	0.06NS	
Isotoma viridis Bourlet	0.2 ± 0.2	1				
Lepidocyrtus cyaneus Tullberg	9.1 ± 3.5	19	10.3*	6.6NS	0.12NS	
Lepidocyrtus lanuginosus (Gmelin)	3.1 ± 1.6	6				
Orchesella cincta (L.)	262.8 ± 61.3	69	**51.4*****	**19.6*****	0.18*	Mainly found on oak and sweet chestnut
Orchesella villosa (Geoffroy)	0.0 ± 0.2	1				
Parisotoma notabilis Schäfer	0.2 ± 0.2	1				
Sminthurinus aureus (Lubbock)	1.1 ± 0.7	4				
Tomocerus vulgaris (Tullberg)	0.3 ± 0.2	2				
Xenylla grisea Axelson	0.5 ± 0.3	3				

Kováč & Miklislová, 2008; Chernov, Kuznetsova & Potapov, 2010, Malmström, 2012) but which has only been recorded reliably two times previously in the UK (National Biodiversity Network, 2016). The near-absence of *Entomobrya intermedia* Brook is noteworthy, since this has been the commonest *Entomobrya* in the bark community of several species of trees in college gardens less than 2 km away (Shaw, 2015). These two *Entomobrya* are visually similar (and would both key out to *E. nivalis* in Hopkin (2007)) but differ in the pigmentation of abdomen segment 4; *E. intermedia* has a roof-shaped mark on the anterior side and a broken line on its posterior end, while *E. nivalis* lacks the roof mark and has a solid line at its base (South, 1961). Although dismissed by Hopkin (2007) as colour variation, sampling across England and Wales has shown that these colour patterns are sufficiently genetically isolated to be considered as good species (Faria, 2015). *Entomobrya intermedia* was not reliably recorded in the UK until 1996, and seems to have undergone a rapid range expansion, suggesting that the Richmond Park woodlands have maintained a relict population of *E. nivalis*, isolated by hundreds of metres of short acid grassland. (The one wood where *E. intermedia* was found on two occasions is site 1, the ornamental wood where plants and potting materials are imported extensively for horticulture.)

The main influence upon abundance was found to be season, with lowest values in summer and highest in winter. Very similar results were reported by Rumble & Gange (2013) for Collembola in green roofs, effectively a man-made suspended soil with extreme annual cycles of heat and desiccation. Collembola numbers peaked in late winter (at 80,000 animals m^2, which exceeds most woodland soils) and dropped to near zero in summer as the substrate dried out. Bowden, Haynes & Mercer (1976) and Shaw (2015) both also found that the biggest catches of most corticolous Collembola were in winter. This pattern is not universal: Shaw (2015) found four bark-dwelling springtails out of 11 to be commoner in summer than in winter. Yoshida & Hijii (2008), studying Collembola in suspended litter of *Cryptomeria* woodland, found an erratic seasonality, with a peak in December 2001 followed by a peak in May 2002 and a minimum in December 2002. They only used these data to test collection efficiencies and did not comment on this anomalous phenology.

It is less clear that the Collembola community composition (rather than numbers) differed between tree species, and the design used was imbalanced with regards to tree species so cannot support firm conclusions. However there were suggestive patterns in the data, notably *E. multifasciata* being generally associated with pine bark and *E. corticalis* with oak. Prinzing (2001) noted increased invertebrate abundance on rough bark, suggesting this was a result of the increase in microhabitats. It is also probable that deeper fissures collect higher quantities of epiphytic vegetation (mosses and algae) or organic detritus, fed on by Collembola (Turner, 1983).

This study found evidence of edge avoidance in the two dominant species of Collembola (*E. albocincta* and *O. cincta*), both when the data were pooled across all seasons (Table 2), and when they were re-analysed by season (Table 3), with the effect especially pronounced in *O. cincta* in winter. Van der Woude & Verhoef (1986) noted that adult *Orchesella cincta* tend to overwinter in tree canopies (and have evolved more cold tolerance than soil-dwelling Collembola). Bowden, Haynes & Mercer (1976) observed that *E. albocincta* preferred core woodland habitat. Edge effects have previously been observed in woodland invertebrates, with both edge-avoidance (Ozanne *et al.* (2000) for spiders, Broadhead (1958) for psocids, Greenslade (1992) for Amphipoda) and edge-seeking having been recorded (Dennis (1997) for beetles and spiders, Thomson & Hoffmann (2009) for parasitic

Table 4. Spearman's correlation coefficients between Collembola and distance from woodland edge, broken down by season. A positive value implies edge avoidance.

Species	May	September	November	December
Total Collembola	0.28	0.19	0.31	0.25
Collembola sp richness	0.06	0.19	0.05	0.27
Entomobrya albocincta	0.37*	0.22	0.16	0.20
Entomobrya corticalis	−0.35	0.03	0.25	0.18
Entomobrya multifasciata	0.35	−0.15	−0.24	−0.14
Entomobrya nivalis	−0.06	−0.02	0.21	−0.01
Orchesella cincta	NA	0.18	0.40*	0.36*

*$p < 0.05$

Table 5. Summary of GLM analysis of log-transformed Collembola density and richness; the models shown had the lowest AIC value of all those available.

Factor	Df	F (density)	F (richness)
Season	3	49.3 ***	52.2***
Wood	3	5.6**	
barkdepth	1	8.3**	2.7NS
distance-edge	1	4.5*	
Season*Wood	9	2.1*	
Residuals	110		

Hymenoptera). Other studies report an absence of edge effects, e.g. Stork, Adis & Didham (1997) for mites, Riutta *et al.* (2012) for woodlice, Shaw *et al.* (2007) for Collembola. This appears to be the first detailed record of an edge effect in corticolous Collembola, and suggests that at least two species benefitted from the shelter of the woodland core.

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SHORT COMMUNICATION

***Lipara pullitarsis* Doskocil & Chvála (Diptera: Chloropidae) new to Britain**. – On 3.iv.2017 two slightly swollen and distorted stems of Common Reed *Phragmites australis* (Cav.) Trin. Ex Steud. were collected from Stodmarsh, Kent, England (TR2261). Each stem contained a puparium which was identified as from *Lipara pullitarsis* Doskocil & Chvála by reference to Chvála *et al*. (1974). The puparia were retained in a well-ventilated and shaded garden shed. One male and one female *L. pullitarsis* emerged from the puparia. Unfortunately, the exact date of emergence was missed, but both were alive on 13.v.2017 and, based on their condition and previous experience of rearing *Lipara*, it was estimated that the male had emerged on about 7.v.2017 and the female on about 10.v.2017. The adult specimens were identified by reference to Chvála *et al*. (1974). The specimens compared well with the descriptions given for *L. pullitarsis* and, although the male genitalia were not dissected, they compared well with those figured for males of *L. pullitarsis*. Both specimens were sent to Laurence Clemons, who dissected the male genitalia and confirmed its identity as *L. pullitarsis*. These are the first records of this species from Britain.

Lipara similis Schiner, *L. lucens* Meigen, and *L. rufitarsis* Loew are also known from Britain. All four species induce galls that distort the apical section of Common Reed. *Lipara pullitarsis* larvae, puparia and adults were separated from the very similar *L. rufitarsis* by Doskocil and Chvála (1971) from specimens collected in (old)